

THE USE OF LATE JURASSIC CORAL GROWTH BANDS AS PALAEOENVIRONMENTAL INDICATORS

by ENZO INSALACO

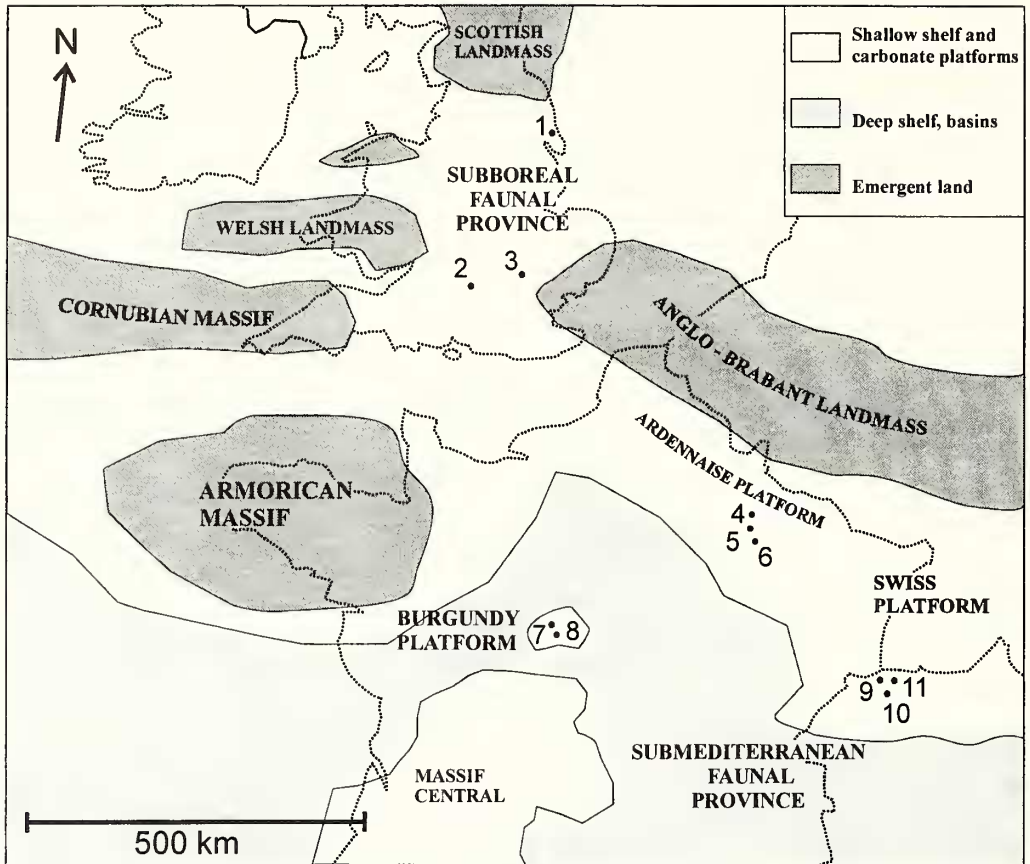
ABSTRACT. A detailed Pan-European sclerochronological study was carried out on two Jurassic corals, *Thamnasteria concinna* (Goldfuss) and *Isastraea explanata* (Goldfuss), the aim of which was firstly, to identify the controls on the deposition of growth bands, on both a regional and local scale, and secondly, to assess the potential value of Mesozoic sclerochronology as a tool for palaeoenvironmental and palaeoclimatic interpretations.

The results indicate that *Isastraea explanata* was the faster growing of the two species with growth rates reaching 4.0 mm/yr where conditions were optimal for coral growth (compared with 2.8 mm/yr for *Thamnasteria concinna* in the same environment). In deep-water environments, growth rates of both corals were considerably lower. This reduction in growth rate is accompanied by a change in growth form from dome-shaped colonies in shallow water to plate-shaped forms in deeper water. Both the reduction in growth rate and change in growth form are interpreted as a response to a reduction in light availability in the deep-water reefs. However, although *Thamnasteria concinna* had the lower growth rate of the two corals it showed a substantially greater variability in its growth rate between different reef environments (up to 50 per cent. of its optimal growth rate).

Data from similar reef types have been compared from different palaeolatitudes in an attempt to identify a palaeoclimatic gradient. No systematic palaeolatitudinal changes in the nature of the growth banding or the growth rate are seen. This is inferred to be a consequence of a Jurassic climate more equable than at present. Reefs from high palaeolatitudes have low growth rates and L/H (low/high) density band ratios. It is suggested that this is a response to low solar radiation. The study therefore shows that these corals can provide useful data for palaeoenvironmental and palaeoclimatic work and should be included, where possible, in such investigations.

GROWTH banding is a prominent feature of many modern corals and since the early 1970s there has been a vast amount of work carried out on their identification and interpretation. However, in their Mesozoic counterparts sclerochronology has received little attention, despite the fact that in many species growth banding is just as pronounced. This is surprising considering its potential value to the study of many aspects of palaeobiology, carbonate production and palaeoclimatology. The aim of this study is to compare the nature of the growth banding and the growth rates of two Late Jurassic corals, *Thamnasteria concinna* and *Isastraea explanata*, in two situations: (1) between *different geographical regions* though within the *same reef type*, thereby normalizing for local environmental effects, such as water depth and sedimentary influx, on growth rate; any difference in growth rates should therefore represent regional differences in factors controlling coral growth, such as temperature, seasonality and solar radiation; (2) between *different reef types* such as deep- and shallow-water reefs within the *same region*; differences in growth rates should be influenced only by differences in the local environment.

The material on which this study is based comes from the Oxfordian reefs of the following regions: Lorraine and Burgundy in France, Oxfordshire, Cambridgeshire and Yorkshire in England, and the Swiss Jura (Text-fig. 1). Within each region, both deep and shallow reef types were sampled. Detailed field work and subsequent laboratory work was carried out to establish the types of reefs and their environmental setting. The basis for such interpretations is based on litho- and



TEXT-FIG. 1. Palaeogeographical map of northern Tethys during the Oxfordian (compiled from Enay and Mangold 1980, and Bradshaw *et al.* 1992). Dots indicate localities sampled. England: (1) Ayton Farm (Yorkshire) (YO); (2) Shellingford Cross-Roads Quarry (Oxfordshire) (OX), (3) Commissioner's Pit, Upware (Cambridgeshire) (UP). France, Lorraine: (4) Haudainville (HA); (5) St Mihiel (MI); (6) Foug (FO). Burgundy: (7) Saussais (SA); (8) Châtel-Censoir (CC). Swiss Jura: (9) Liesberg (LI); (10) Courtételle (CO); (11) St. Ursanne (UR).

biofacies analysis on both macro- and microfacies scales. The coral reefs chosen for this study can be placed into four broad categories that represent end-members in a complete spectrum of reef types in terms of their water depth and siliciclastic content. Differences in the environmental conditions between different reefs of the same reef type are negligible when compared with the environmental differences between reefs of different reef types. Brief descriptions of the reef types discussed in this study are given below; for more detailed descriptions and interpretation of reef localities, see Pumpin and Woltersdorf 1965 (UR and LI); Ali 1977, 1978, 1983 and Hitchings 1981 (YO, OX, UP); Geister and Lathuilière 1991 (MI, HA, F1 and F2); Menot 1991 (SA and CC). (See Text-fig. 1 for locality abbreviations.)

1. Deep-water reefs: deep-water microsolenid biostromes

Reefal unit dominated by an interlocking framework of platy corals in a bioclastic wackestone. Coral fauna dominated by microsolenids such as *Microsolena*, *Dimorpharaea* and *Comoseris*. Two reefal facies may be identified: (a) a siliciclastic-rich facies dominated by *Dimorpharaea* occurring

within marly, clay-rich sediments (study examples F1, LI); (b) a siliciclastic-poor facies dominated by *Microsolena* occurring within pure limestones (study examples UP, F2, CC). Red algae are notably absent from both these reef sub-types. There is no evidence of current or wave action suggesting that reef development occurred well below normal wave base. Storm horizons are absent. These biostromes are the first coral-dominated reefal structures to develop in comparatively deep water aggradational sequences and often overlie more basal sponge- and ammonite-bearing facies. The main environmental controls on the development of these reefs were the extremely low light levels associated with their relatively deep bathymetric position and, in some cases, muddy water (turbidity) from the high clay fraction of the siliciclastic influx (Geister and Lathulière 1991; Menot 1991; Leinfelder 1993, 1994; Leinfelder *et al.* 1994). Study examples from England and continental Europe do not show major structural or compositional differences.

2. Shallow-water reefs

Low siliciclastic influx (study examples from continental Europe: MI, HA, SS, CO, UR): clean, shallow-water patch-reefs. High diversity coral patches have a rich association of corals (both in terms of taxa and growth forms). Dome-shaped and branching, ramose colonies dominate. No single coral taxon dominates the fauna. Red algae are present and can be locally common. Intra-reef sediments are clean, coarse-grained bioclastic packstones. These reefs have a high bioclastic component. Inter-reef sediments are also coarse grained bioclastic packstones with coated grains being common. Grain reworking and the development of coated grains suggest that current and wave action were present and water depths were very shallow. There is evidence that storm events were common. Light levels were not a limiting factor in the development of these reefs (Geister and Lathulière 1991; Menot 1991). The study example from Yorkshire, England (YO) is different, although it is also developed in siliciclastic-free, very shallow water. The reefs occur as low diversity coral patches. Dome-shaped colonies of *Thamnasteria concinna* dominate. Intra-reef sediments are coarse grained oo-bioclastic packstones. Inter-reef sediments are oolitic grainstones. The sedimentological criteria again suggest that water depths were very shallow and above normal wave base. As with the continental examples, light levels were not a limiting factor in the development of these reefs (Hitchings 1981).

High siliciclastic influx (study example OX): low diversity coral thickets. Typical coral genera are *Thamnasteria*, *Thecosmilia*, *Isastraea* and *Fungastraea*. Siliciclastic lenses and bands are well developed and common. Sedimentological criteria suggest deposition in very shallow water and above normal wave base. Storm horizons are frequent. The main controlling factor in the development of these reefs was the frequency and degree of siliciclastic influx (Ali 1977, 1978, 1983).

NATURE OF THE GROWTH BANDING, AND METHODS

Thamnasteria concinna and *Isastraea explanata* were chosen for this study because they are almost ubiquitous in Late Jurassic reefs but, more importantly, consistently show pronounced, well preserved growth banding; thus the large numbers of specimens needed for such a study were available. Furthermore, the quality of the growth banding was such that accurate measurements could be taken in the field by using silicon carbon grinding paper to grind down the surface to 800 grade. This method proved very successful on the soft limestones and increased the total size of the data set considerably. More detailed analysis of the banding regarding septal thickness and dissepiments distribution was carried out on selected polished slabs and thin sections with the use of optical microscopes. All growth rate measurements were measured in millimetres (mm) and were estimated to 1 decimal place.

Distinct growth banding is visible in longitudinal section in many of the specimens studied and is identical to the seasonal high- (H) and low (L) -density bands present in many modern corals and assumed to have developed in the same way (Knutson *et al.* 1972; Ali 1984; Geister 1989; Le Tissier and Scrutton 1993). The annual (seasonal) nature of these pairs of bands has been thoroughly

confirmed by comparison with chronologies from radioactivity labelled environments (Knutson *et al.* 1972; Knutson and Buddemeier 1973; Buddemeier *et al.* 1974; Moore and Krishnaswami 1974; Noshkin *et al.* 1975), by the general agreement between radiographic growth rates and those from conventional radiometric dating (Dodge and Thomson 1974; Moore and Krishnaswami 1974), and by the general agreement with real-time measurements (Buddemeier and Kinzie 1976, table 2). The banding is depicted by alternating regions of thicker septa with more numerous dissepiments (high density band), and a band of thinner, less well developed septa with fewer dissepiments (low density band) (Pl. 1, figs 1–3; Pl. 2, figs 1–2; Pl. 3, figs 1–3).

On each colony the following measurements were recorded from five consecutive L/H density couplets: (1) spacing of the L/H density couplet (growth rate); and (2) the L/H thickness ratio. For each sample site, the arithmetical mean of the growth rate and L/H ratio for each species was calculated. The standard deviation for the growth rate was also calculated in order to indicate the degree of growth rate variability for a given species at each locality.

Two problems are encountered when measuring the growth rate on individual colonies. Firstly, there can be variations in growth rate along the section. Care is needed in assuring that the orientation of the section is truly vertical. Oblique sections give erroneously high measurements. This problem is compounded in some colonies by the fact that the corallites do not show straight vertical growth. This problem is especially pronounced in colonies that show mammilose growth surfaces. This results in sections that are in part vertical and in part oblique. This is illustrated in Plate 2, figure 2 where the bottom left of the figure shows an almost transverse section whereas the rest of the section is effectively vertical. Care needs to be taken to take measurements only from the fully vertical sections. The growth forms of the two species chosen for the study are tabular to domal with planar top surfaces, which suggests that divergent corallite growth was not marked. However, where this was marked, with a resultant axiality in growth, the axial growth rate was taken. Marked axiality was very rare and only encountered in three colonies (Pl. 1, fig. 3).

Another problem is one of the continuity in the definition of the low and high density bands. Even in colonies that are generally well preserved, there are often small areas of the colony that have undergone greater recrystallization than others, with a resultant loss in the sharpness of the bands. These areas were avoided when taking measurements. For example, in Plate 2, figure 2, the area which was measured is the far right and top of the specimen. The central area, which has experienced a greater amount of recrystallization, was not measured.

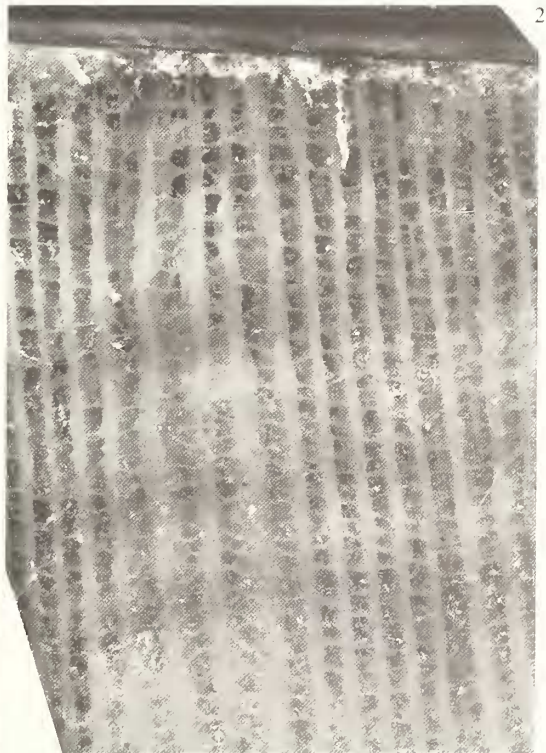
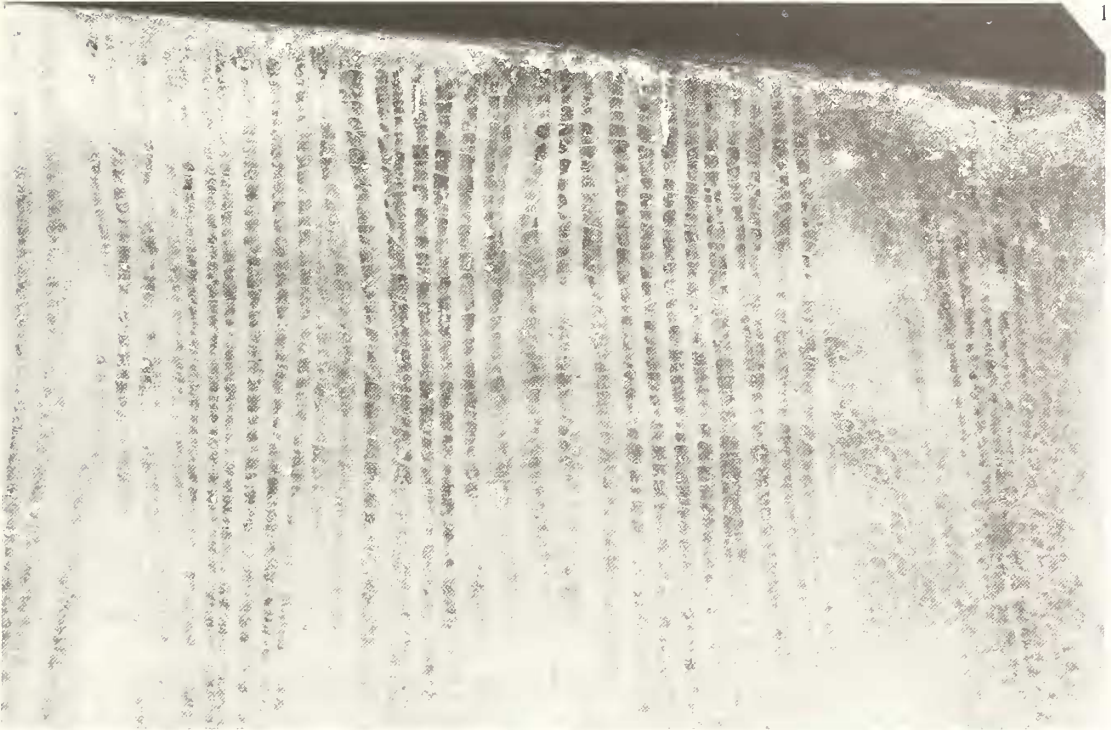
For each species, per sample locality, the distinctness of the L- and H- density was also recorded. This is an indication of the visual contrast in a L/H density couplet between the low density band and the high density band. Where the visual contrast between the two bands is high (high distinctness), the L/H couplets are easier to distinguish. The distinctness was recorded using an arbitrary scale of 1 to 5 (1 = low, 5 = high). This is based on a general assessment of all the colonies for each species per sample locality.

In none of the reefs studied were there any lateral or vertical changes in litho- or biofacies that

EXPLANATION OF PLATE I

Figs 1–2. *Isastraea explanata* (Goldfuss); BU 100501; Liesberg Member (Oxfordian); Liesberg, Swiss Jura; polished slab from a deep-water microsolenid biostrome. 1, growth banding defined by high (light) and low (dark) density bands; growth rate *c.* 2.7 mm/yr; $\times 7$. 2, details of the high and low density bands shown in Figure 1. In the high density band, most septa are thicker with more numerous and closely spaced dissepiments. In the low density band, the septa are less well developed with fewer dissepiments; $\times 9$.

Fig. 3. *Thamnasteria concinna* (Goldfuss); BU 100101; Coral Rag (Oxfordian); Shellingford Cross Roads, Oxfordshire, England; polished slab from a shallow water reef; well developed, pronounced growth banding; axial growth rate *c.* 2 mm/yr. Note the marked distinctness of the high and low density bands, and the low/high density band ratio (approx. 0.5); $\times 6$.



INSALACO, *Isastraea*, *Thammasteria*

could be attributed to changes in the environment. Therefore, since there is no evidence of ecological succession or zonation within these reefs, an indiscriminate sampling procedure over the total exposure of each reef complex was used to select colonies for measurement. Only well preserved colonies, where at least five consecutive L/H density couplets could be measured, were selected. The whole study is based on measurements of 875 L/H density couplets from 175 colonies. However, it should be noted that although, with one exception, both corals were present in all the reefs studied, they are not equally present in these different reefs. For example, the reef at Ayton Quarry, Yorkshire, is an almost monospecific patch of *Thamnasteria concinna* with only one colony of *Isastraea explanata* found (which has been excluded from the analysis because of the small sample size). Hence, at this locality, the analysis of *Thamnasteria concinna* is based on a large sample size (20 colonies). Conversely, in many of the reefs in France and Switzerland, these two corals are rare and generally less than eight well preserved colonies would be measured. In general, *Isastraea explanata* and, especially, *Thamnasteria concinna* became less dominant in the more southerly reefs (Bertling 1993).

Repositories. The author's collections are housed in the School of Earth Sciences, University of Birmingham (BU) and The Natural History Museum, London.

RESULTS

Growth rates

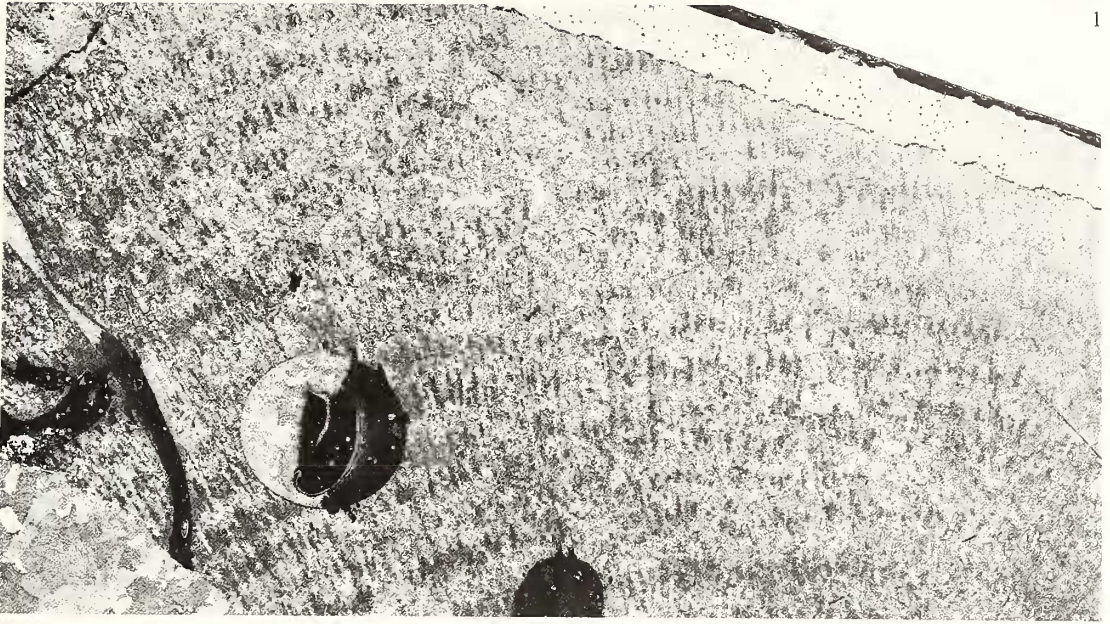
Table 1 and Text-figures 2–5 summarize the results of the study. Text-figure 2 shows the growth rate of the corals in the same reef type in different regions. In both plots, there is a weak trend, in both species, of decreasing growth rate with increasing palaeolatitude. The highest values were encountered in the Swiss Jura and the lowest in England. In both species, this trend is more marked in the shallower water facies where values range from 4 mm/yr (Swiss Jura) to 2.5 mm/yr (British Corallian) in *I. explanata*; and 2.8 mm/yr (Swiss Jura) to 0.8 mm/yr (British Corallian) in *T. concinna*. In the deeper water facies, this variation is less pronounced, with values ranging from 2.8 mm/yr (Swiss Jura) to 2.2 mm/yr (British Corallian) in *Isastraea explanata*, and 1.5 mm/yr (Swiss Jura) to 0.8 mm/yr (British Corallian) in *Thamnasteria concinna*. However, these decreases in growth rate are not significant at the 95 per cent. confidence level since the difference between adjacent points is less than 1.96 standard deviations. Also evident on the shallow-water plot (Text-fig. 2A) is a sharp decrease in the growth rate, again in both species, between the continental and the English localities. This shift from 3.6 to 2.5 mm/yr for *Isastraea explanata*, and 2.7 mm/yr to 1.3 mm/yr for *Thamnasteria concinna* between Haudainville (Lorraine, France) and Oxfordshire (England) is well above 1.96 standard deviations and therefore significant at the 95 per cent. confidence level. This feature is not visible in the deeper water facies. Text-figure 2B also shows that the difference in growth rate, for a given region, between *Thamnasteria* and *Isastraea* is greater in the deeper water facies.

Text-figures 3A and 3B illustrate the variation in the growth rates in the two corals between shallow- and deeper water facies. Comparing Text-figure 3A with 3B, it is immediately apparent that, in general, *Thamnasteria concinna* shows a greater variability in growth rate than *Isastraea explanata* between extreme reef types. It is also clear from Text-figure 3A, and to a lesser extent 3B, that the difference in growth rate between shallow and deeper water reefal units is much greater in

EXPLANATION OF PLATE 2

Figs 1–2. *Thamnasteria concinna* (Goldfuss); Coral Rag (Oxfordian). 1, BU 100121; Ayton Farm, Yorkshire, England; photomicrograph of unstained thin section; $\times 7$. 2, BU 100102; Shellingford Cross Roads, Oxfordshire, England; photomicrograph of stained thin section; $\times 5$.

1



2



TABLE 1. Summary of results. G.R., arithmetical mean growth rate (mm/yr); L/H, low/high density ratio; DIST, distinctness value; SD, standard deviation of the mean growth rate; NO, number of colonies measured. Approximate palaeolatitude of each location is indicated in parentheses.

Location	<i>Thamnasteria concinna</i>					<i>Isastraea explanata</i>				
	G.R.	L/H	DIST.	SD.	NO.	G.R.	L/H	DIST.	SD.	NO.
Yorkshire (YO; 39° N)	0.8	0.4	5	0.12	20	—	—	—	—	—
Oxfordshire (OX; 36.5° N)	1.3	0.6	5	0.11	11	2.5	0.5	5	0.28	8
Cambridgeshire (UP; 37° N)	0.8	0.5	5	0.11	8	2.2	0.5	5	0.35	4
Foug 1 (F1; 34° N)	1.1	0.4	5	0.15	13	2.6	0.6	5	0.29	7
Foug 2 (F2; 34° N)	1.3	0.5	5	0.11	10	3	0.7	4	0.31	5
Haudainville (HA; 34° N)	2.7	1.4	2	0.18	4	3.6	1.3	1	0.32	3
St. Mihiel (MI; 34° N)	2.4	1.2	2	0.17	5	3.4	1.3	3	0.27	3
Châtel-Censoir (CC; 33° N)	1.2	0.7	1	0.13	7	3.1	0.5	1	0.27	5
Saussois (SA; 33° N)	3	1.4	1	0.12	6	3.7	1.6	1	0.29	4
Liesberg (LI; 32° N)	1.5	0.5	5	0.14	17	2.8	0.5	5	0.26	14
Courtételle (CO; 32° N)	2.5	1.7	1	0.12	8	3.8	1.4	2	0.3	3
St. Ursanne (UR; 32° N)	2.8	1.3	2	0.12	6	4	1.5	2	0.31	4

Lorraine, Burgundy and the Swiss Jura, than in England, this being especially pronounced in *Thamnasteria concinna* (Text-fig. 3A).

Low/high (L/H) density band ratio

The L/H ratios of the corals studied are shown in Text-figure 4. L/H ratios range from 0.4 in Yorkshire to 1.7 in the Swiss Jura. L/H ratios of *Thamnasteria concinna* and *Isastraea explanata* do not seem to be significantly different, nor do they show any significant regional variations. The L/H ratio results can be grouped into three clusters.

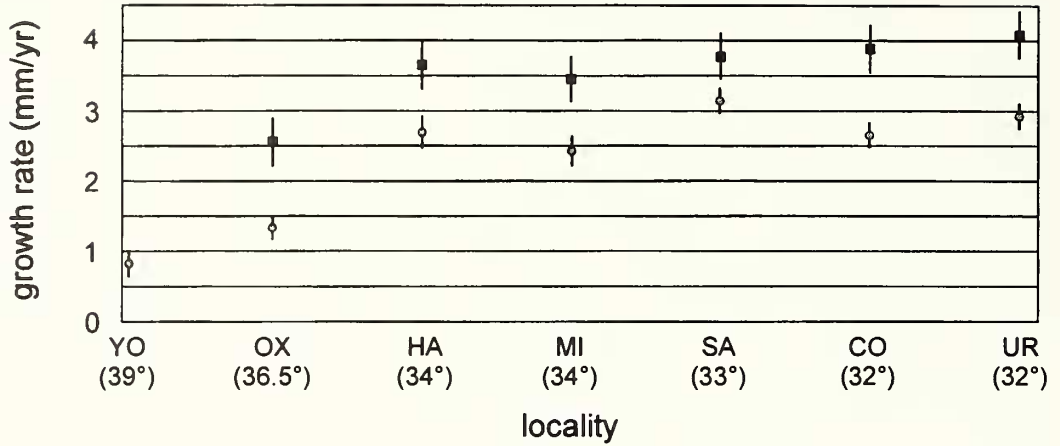
1. Colonies that show L/H ratios greater than 1.2 occurring in the shallow-water facies (Lorraine, Burgundy, Swiss Jura);
2. Colonies that show L/H ratios less than 0.7 occurring in the deep-water facies (Upware, Foug, Châtel-Censoir, and Liesberg);
3. Colonies occurring in shallow water though having an L/H ratio of less than 0.7 (Yorkshire and Oxfordshire).

EXPLANATION OF PLATE 3

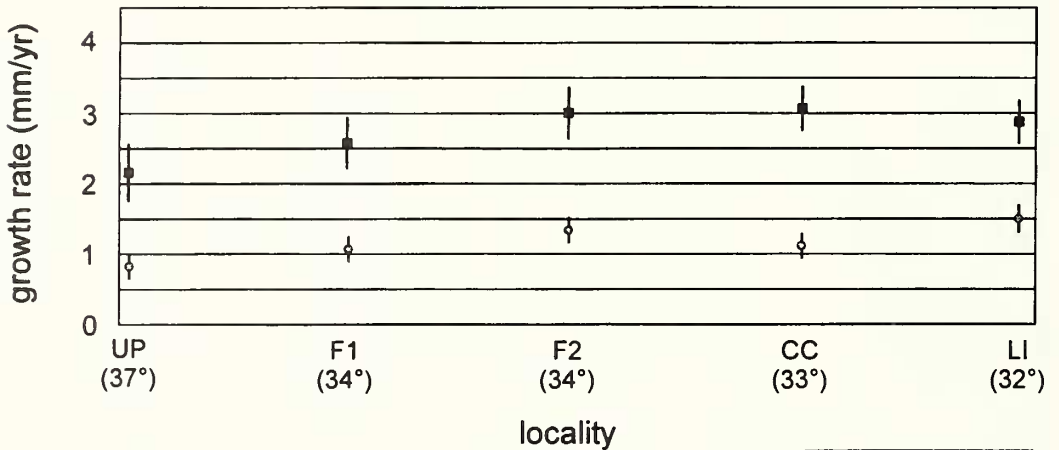
Figs 1–3. *Thamnasteria concinna* (Goldfuss); BU 100401; Lower reef complex (Oxfordian); Châtel-Censoir, Burgundy, France; photomicrograph of unstained thin section from a deep-water microsolenid biostrome, showing thinning and thickening of skeletal relics and their neomorphic replacement by calcite (the light coloured coarsely crystalline material); low density bands (dark zones) show best preserved septa since they were originally thinner with fewer dissepiments resulting in less neomorphic replacement. Dark material between the septa is likely to represent early marine peloidal cements; Fig. 1, $\times 15$; Fig. 2, $\times 40$; Fig. 3, $\times 85$.
Fig. 4. *Thamnasteria dendroidea* (Lamouroux); BU 100301; Upper reef complex (Oxfordian); Haudainville, Lorraine, France; polished slab; axial growth rate c. 13 mm/yr; $\times 1.5$.



A. SHALLOW-WATER REEFS



B. DEEP-WATER REEFS



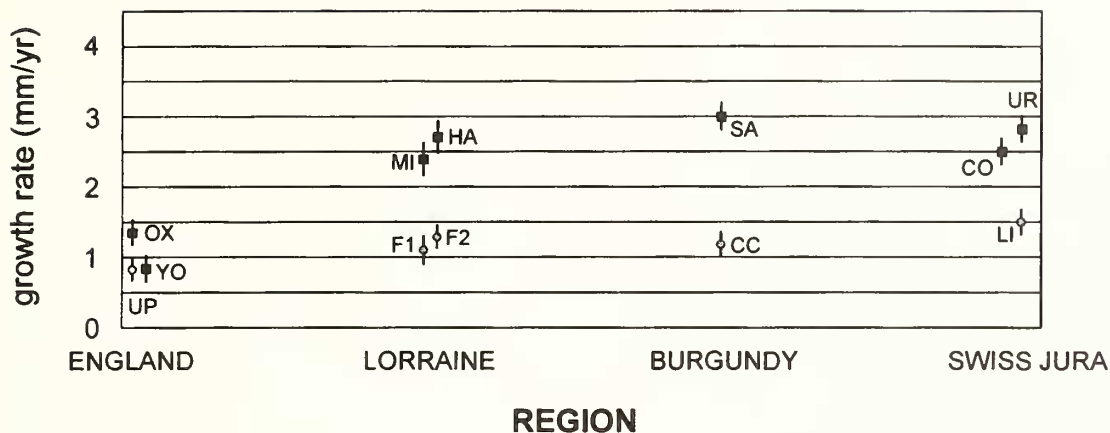
■ *I. explanata*
○ *T. concinna*

TEXT-FIG. 2. Variation in growth rate (mm/yr) between *Thamnasteria concinna* and *Isastraea explanata* in shallow (A) and deep water (B) reefs. The points plotted are the arithmetical means of all the measurements collected for each species per locality. Vertical line represents ± 1 standard deviation. Also indicated in parentheses is the approximate palaeolatitude of each location in °N.

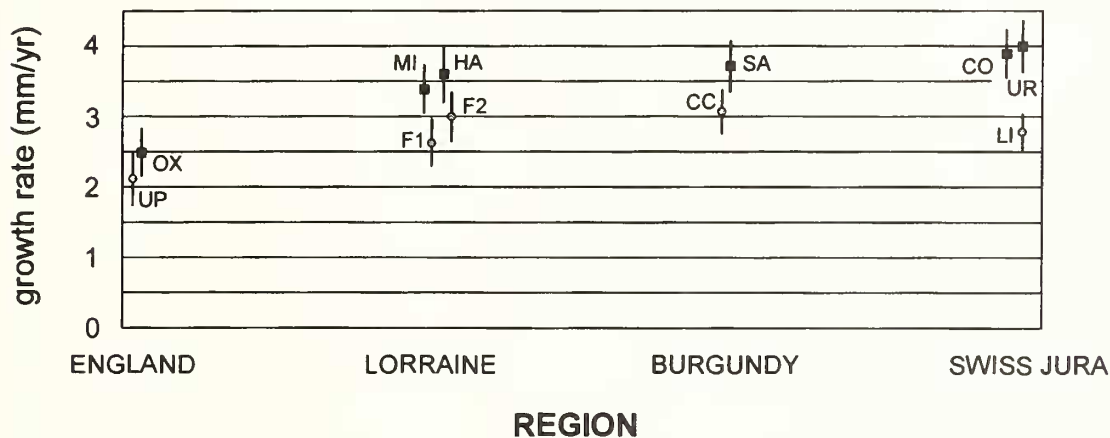
Distinctness (D)

D does not seem to vary systematically between the two species. Not all the colonies show distinct growth banding; however, this phenomenon is also encountered in modern corals (Weber and White 1974; Huston 1985). Diagenesis has probably altered the natural distinctness to an unknown extent but, since these reefs have undergone similar diagenetic histories, it seems probable that the relative distinctness has remained similar to the original values. D was extremely high (5, 4) in all

A. *Thamnasteria concinna*



B. *Isastraea explanata*



■ SHALLOW-WATER REEFS ○ DEEP-WATER REEFS

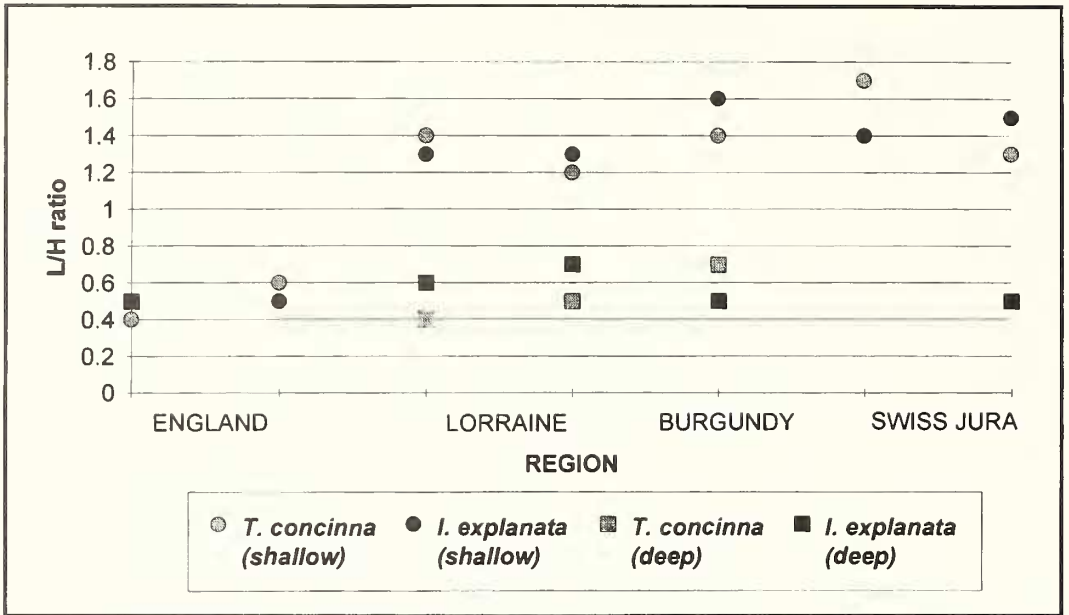
TEXT-FIG. 3. Variation in growth rate (mm/yr) between shallow and deep water reefs for *Thamnasteria concinna* (A) and *Isastraea explanata* (B). The points plotted are the arithmetical means of all the measurements collected for each species per locality. Vertical line represents ± 1 standard deviation.

the English localities with outside England only Liesberg showing a similarly high value (Pl. 1, fig. 3). The European localities generally show low D values (2, 1) (Text-fig. 5).

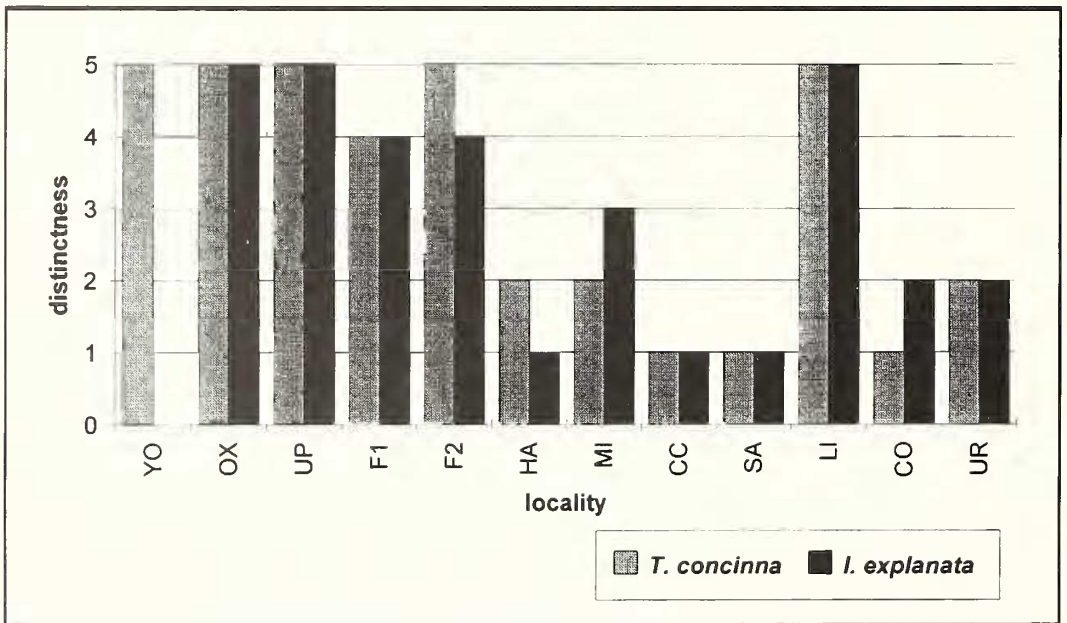
DISCUSSION

Growth rates

The weak general trends shown on Text-figures 2A and 2B are notable by their insignificance at the 95 per cent. confidence level. Since these plots are comparing corals from the same reef type across different regions (2A for shallow-water reefs and 2B for deep-water reefs), differences in growth rate



TEXT-FIG. 4. Low/high density ratios from both reef types and all localities for both species. The points plotted are the arithmetical means of all the measurements collected for each species per locality.



TEXT-FIG. 5. Distinctness values for the low- and high-density couplets.

should be independent of local environmental controls and should reflect more regional changes in climatic (temperature, solar radiation and seasonality) and/or oceanographic factors (Glynn 1977). One might therefore speculate that with an increase in palaeolatitude, there would be a decrease in regional average temperature and solar radiation, consequently resulting in a decrease in growth

rate. This is not revealed in the data. However, it has been well established that the Jurassic climate was more equable than at present and therefore environmental gradients not as steep (Hallam 1975, 1984, 1993). This allowed a general spread of coral reefs as far north as Scotland which lay at approximately 43° N; this contrasts strongly with the present-day limits of reef growth which lie approximately 35° N and S of the equator (Rosen 1981). Hence, the lack of large variations in growth rates between the regions studied, all of which lie within a broad mid-latitude climatic belt, might be accounted for by the small difference in palaeolatitude between adjacent localities, and the equable palaeoclimatic regime. Growth-rate data are not yet available for reefs located farther south (such as the Portuguese and Slovenian reefs) or farther north (such as the Helmsdale corals in north Scotland). These areas would provide corals that grew outside this climatic regime and therefore differences in their growth rate might reflect climatic differences. What is now clear is that this climatic signal would be best searched for in corals such as *Thamasteria concinna* and in shallow-water reefs with low siliciclastic influx, since these were evidently the most sensitive to environmental changes (see below).

The low growth rates recorded in the Yorkshire reefs (YO) are, however, significant. The difference in growth rate between Yorkshire and the continental European reefs, which developed in similar shallow-water siliciclastic free environments, is very marked (approximately 1.5 mm). As explained above, there is clear evidence to suggest that climatic gradients between these regions were not steep, and hence were unlikely to be responsible for the difference in growth rate. One possible explanation for the reduced growth rates of the corals from the Yorkshire reefs is the reduction in annual solar radiation as a consequence of their relatively high palaeolatitude. In this respect, it is interesting to note that it has been shown that most Mesozoic and Cenozoic shallow shelf carbonates occur within the sub-tropics, 5–35° N and S (Ziegler *et al.* 1984). Evidently, the carbonate belt did not shift northwards during warmer periods such as the Jurassic, suggesting that simple climatic considerations are not enough to explain coral distribution. However, year-round solar radiation falls markedly at about 35° from the equator, the present poleward limit of Bahamian-type environments. Ziegler *et al.* (1984) suggested that it is this latitudinally induced drop in light intensity which limits depositional systems that rely on algal-symbiotic fixation of calcium carbonate, either directly or indirectly, to within these latitudes. It is likely that this decrease in solar radiation adversely affected growth band development in the corals of Yorkshire, which lay approximately 39° N, resulting in low growth rates (Smith *et al.* 1980).

Another interesting feature of Text-figure 2A is the sharp decrease in the growth rate between Haudainville and Oxfordshire. This decrease is likely to be due to the increase of seasonal runoff and the adverse effects that this has on coral growth (increased sedimentation, increased turbidity and possibly the adverse effects of increased nutrient flux). This feature is absent in the deeper water reefs since all of these reefs shared similar ambient conditions. Text-figure 2B shows that growth rates in deeper water reefs show little variation between locations. This lack of regional variation may be explained by the fact that these deep-water biostromes developed in conditions of low light and high sedimentation with its associated high turbidity, hence any regional signal is probably masked by the strong local environmental overprint.

Text-figures 3A and 3B illustrate the variation in growth rates in the two corals between shallow and deeper water facies. Growth rates in the deep-water biostromes are likely to represent the slowest possible growth rates for these corals since these reefs developed in comparatively stressful environments. Any further deterioration in environment, such as would be caused by increases in sedimentary influx, turbidity and hence decreases in light, are likely to result in coral mortality rather than a further reduction in growth rate. On the other hand, growth rates in the shallow-water reefs, especially on the clean carbonate platforms of Burgundy and the Swiss Jura (Text-fig. 1) which provided near optimal conditions for coral growth, are likely to represent values close to the maximum linear extension possible for these corals. This contrast is reflected by a dramatic decrease in growth rate from shallow- to deep-water in all regions and in both species (Text-figs. 3A and 3B). The decrease in growth rate is accompanied by a change in growth form from dome-shaped colonies in shallow-water settings to flat platy forms in deep-water. These results are analogous to those of

studies carried out at Discovery Bay, Jamaica (Huston 1985), in which four out of six coral species (*Porites astreoides*, *Montastrea annularis*, *Colpophyllia natans* and *Siderastrea siderea*) significantly decreased their growth rate over a 1–30 m depth interval. Also documented in these corals were changes in growth form from dome- to plate-shaped colonies along the same depth gradient. This was especially pronounced in *Montastrea annularis* as was the change in growth rate. Huston concluded that the major control over both these changes (form and growth rate) is decreasing light levels, which reduces calcification rates significantly. Other studies on the relationship between depth and growth rate on present-day reefs come to similar conclusions (Goreau 1959, 1963; Goreau and Goreau 1959; Goreau and Wells 1967; Baker and Weber 1975; Dustan 1975, 1979; Highsmith 1979). In the Jurassic deeper water, low light intensity reefs, further evidence of the suppression of the coral calcification process comes from: (1) a poorly developed wall structure in *Isastraea explanata*, resulting from a reduction in the number and density of dissepiments; (2) the dominance in these reefs of microsolenids which are well adapted to environments where calcification is hindered (Leinfelder 1993, 1994; Leinfelder *et al.* 1994).

Text-figures 3A and 3B also clearly show that the difference in growth rate, in both corals, between shallow- and deep-water facies is greater in continental European localities than in England. This simply reflects the fact that the environmental contrast between the shallow- and deep-water facies was much greater in the European areas. In Europe, the shallow-water reefs developed in near ideal conditions for intense reef growth, i.e. warm, well lit water on clean shallow-water carbonate platforms. The deep-water reefs, on the other hand, grew at the environmental limits of reef growth in conditions of extreme low light and in some cases high turbidity. The situation in England was clearly different, although the deep-water reefs developed in equally poor conditions resulting in equally low growth rates, the shallow-water reefs did not develop in the same ideal environments as their European counterparts due to sedimentary influx and, in the more northerly locations (such as Yorkshire), the possible effects of reduced solar radiation; as a result, their growth rates are not as high.

What is also clear from Text-figures 3A and 3B is that *Thamasteria concinna* shows greater variability in its growth rate than *Isastraea explanata* (though *Isastraea explanata* shows more intra-colony variability, as reflected by its larger standard deviation), both between different reef types and also between different regions. This is consistent with the suggestion that *Thamasteria concinna* possesses an extremely plastic ecomorphic behaviour (Geister and Lathuilière 1991; Bertling 1993). In deeper water environments, such as the deep-water microsolenid reef studied, this coral develops a marked platy growth form. In shallower water, it exhibits a much more massive appearance. Furthermore, if one accepts that *Thamasteria dendroidea* (Lamouroux) is simply a branching morphotype of *Thamasteria concinna*, as is now believed (Geister and Lathuilière 1991; B. Lathuilière, pers. comm. 1993), then it developed a branching habit in very shallow, quiet, water. What this study seems to show is that this plasticity in the growth form of *Thamasteria concinna* is paralleled by a plasticity in its growth rate. *Thamasteria concinna* seems to have varied its growth rate considerably in response to growing in a wide variety of different reef environments. This high degree of ecomorphic and ecophysiological plasticity suggests that *Thamasteria concinna* was an *r*-strategist, hence its dominance in the unstable reef environments of the Sub-Boreal Province (Bertling 1993). In fact, there would appear to be an intimate relationship between plasticity in growth form and plasticity in growth rate, since differences in growth form are a function of contemporaneous intra-colonial variations in growth rate, though sites of budding are also important. Thus, platy forms developed when all the corallites on the surface of the coral grew at the same rate, whereas in dome-shaped forms, the corallites axial to the dome grew significantly faster than the peripheral corallites. In extreme cases, branching colonies developed where there was a number of very localized 'hot spots' in coral growth which subsequently exhibited extremely fast growth and formed branches. In the case of *Thamasteria concinna* (type 'dendroidea'), branch growth rate could reach 13 mm/yr (approximately ten times the growth rate of their deeper water platy counterparts) (Pl. 3, fig. 4). A similar relationship seems to exist in present-day corals; for example, *Montastrea annularis* shows the highest variation in growth rate between deep- and

shallow-water environments, but also shows the most marked variation in growth form between these extreme water depths (Huston 1985). It is interesting to note in this respect that although *Isastraea explanata* shows a higher growth rate of the two species studied, its inter-colony variation is relatively small, which is paralleled by its limited ecomorphic plasticity (*Isastraea* never develops a branching ramose form and only shows moderate morphological variation between thick plates and large heads). This suggests therefore that the ability for a coral to vary its growth rate substantially may be a prerequisite for the coral to attain a high degree of ecomorphic plasticity.

From 175 colonies studied (both *Isastraea* and *Thamasteria*), no evidence of determinate growth, as hypothesized by Barnes (1973) for massive corals, was found. The present study is consistent with other studies (Buddemeier 1974; Dodge *et al.* 1974; Buddemeier and Kinzie 1976; Hudson *et al.* 1976; Highsmith 1979).

Low/high density ratio

The L/H ratios clearly fall into three groups. Ali's (1984) study of growth banding in the English Oxfordian showed that the corals from the reefs of the Sub-Boreal Province had relatively low L/H values (generally less than 1.0), compared with the values of present-day shallow-water corals in the Indo-Pacific and the Caribbean which are generally greater than 2.0 (Weber *et al.* 1975; Buddemeier and Kinzie 1976). The present study corroborates Ali's (1984) observation, with observed L/H ratios of 0.4–0.6. The argument put forward by Ali suggests that the reason for these low values is reduced light levels resulting from high local turbidity. This is probably a very significant factor; however, one must not discount increased cloud cover for a reduction in solar radiation, especially for a more northerly location such as Yorkshire. This has been shown to be of importance by a study on present-day growth rates in corals from the tropical Pacific (Buddemeier 1974). In Buddemeier's (1974) study, a positive correlation between the high density bands and lowered light levels (resulting from increased cloud cover) was identified. The latitude-related reduction in solar radiation as implied by Ziegler *et al.* (1984) is also likely to have affected growth band development in the corals of the Yorkshire reefs.

The present study also demonstrates that where strong siliciclastic influx is not present, such as in the shallow-water reefs of Lorraine, Burgundy and the Swiss Jura, L/H ratios increased (larger low density band) and approach the value of present-day corals, although they are still persistently and considerably lower. One explanation for this inconsistency between modern and Mesozoic values is again related to the relatively high palaeolatitudinal location of these reefs (lying approximately between 32° and 39° N). This would have had two adverse effects on coral growth: (1) although temperature gradients were not as steep as at present, temperatures in these high palaeolatitudes may still have been lower than those in present-day tropical reef-growing areas; (2) latitude-related reduction in solar radiation. These two factors would have inhibited extensive growth of the low density bands. More data from around the palaeoequator are needed to confirm this. From these low palaeolatitudes, it is predicted that L/H ratios will be significantly greater than found in the present study and would compare well with present-day values.

The third cluster of values is from the deep-water reefs, with values below 0.7. This again may be explained by applying a model which invokes a negative correlation between density and light levels. Although it is still unclear which factors control the density variations, there is strong evidence to suggest that the density bands correlate negatively with light level as well as temperature. Indeed, it has been demonstrated that L/H ratios decreased with depth in a study of the present-day corals of the Enewetak Atoll (Highsmith 1979). This suggests that light is the more important factor governing the deposition of these density bands, rather than temperature, which does not decrease as rapidly with depth.

Distinctness

It has been established that in modern corals the low density band is deposited during the summer when the linear extension is greater and consequently the skeletal structure more open, and the high

density band is produced during the winter when the process is reversed (Buddemeier 1974). Although it is clear that the above process is the cause of the low and high density couplet, there is still debate as to which precise aspect of the seasonality is driving the process. It seems likely that it is a result of a complex interplay of factors, such as temperature, light and reproductive state, making accurate environmental deductions based solely on band distinctness more difficult (Tudhope 1994). Nevertheless, the model implies that where the difference between the summer and winter seasons is large (i.e. a highly seasonal climate), the gross difference between the density bands, and consequently their visual appearance, should also be correspondingly large, i.e. the greater the seasonality the greater the distinctness, all other factors being equal. If one accepts this model for the production of growth bands for Mesozoic corals, the data would suggest that at this time the study area was in a highly seasonal climatic belt, as reflected by pronounced growth bands. This would be consistent with both computer models and empirically based models for Late Jurassic climates that suggest that northern Tethys experienced a strongly seasonal climatic regime (Moore *et al.* 1992a, 1992b; Valdes and Sellwood 1992; Hallam 1993). This reasoning is similar to that used by Ma (1934, 1958) who used this technique with Palaeozoic corals to locate the position of the equator relative to drifting continents at various times during the Palaeozoic. A subsequent reinterpretation of Ma's (1934) data, in the light of continental drift theory, by Fischer (1964) shows that the method is reliable. In a similar study, though on Lower Jurassic to Lower Tertiary fossil tree trunks, Creber and Chaloner (1984) were able to recognize a broad equatorial zone ranging in latitude from approximately 30° N to 30° S, in which annual growth rings are either absent or very poorly developed. Either side of this zone, annual growth bands were more pronounced and well developed, and were interpreted as suggesting a strongly seasonal climate.

Text-figure 4 clearly shows that values of D varied not only between different areas but also between different reef types within the same region. This pattern cannot be explained by applying a simple seasonality model. Looking at the data in more detail one finds that the following localities have high D values: Ayton Farm, Shellingford Cross-Roads Quarry, Upware, Foug, and Liesberg, whereas for St Mihiel, Haudainville, Châtel-Censoir, Saussois, St Ursanne and Courtételle distinctness is low. Taking account of the lithofacies and palaeogeography, a very clear pattern emerges: the localities with high values of D are those that have a high siliciclastic component and/or are strongly influenced by nearby land masses; localities with low D values occur in very pure carbonate environments with very little influence from land masses. So, although seasonality does not seem to influence the degree of distinctness directly, its indirect influence is nevertheless considerable. Seasonal increases in precipitation and wind energy produced high runoff resulting in large influxes of sediments, and possibly nutrients, into the surrounding sea. Where this coincides with areas of reef development, the corals show greater contrast in their high and low density bands, resulting in higher D values. Further evidence for such a pronounced seasonal process is provided by thin veneers of sediment found at the top of the low density bands in a number of specimens from the English Oxfordian. A similar process was invoked for the corals of the Great Barrier Reef by Boto and Isdale (1985). They suggested that there was a strong correlation between the intensity of the fluorescence in the coral skeleton, and the seasonal pattern of rainfall and runoff from the adjacent Australian landmass. They suggested that the fluorescence in the coral skeleton is caused by organic acids of terrestrial origin that are washed in during periods of high runoff.

CONCLUSIONS

Palaeogeographical and palaeoenvironmental settings, in combination with the palaeoclimatic regime, have been found to exert a strong control on the nature of growth banding, and also the rates at which these bands were deposited. The combination of strong seasonal rainfall and proximity to land masses resulted in lowered growth rates and L/H ratios, though increased distinctness values. Where reef development was distal to sediment source areas, the effect of seasonality was much less marked; consequently, distinctness values decreased but L/H ratios and

growth rates increased. All these changes were more pronounced in the shallow-water reefs, which seemed to have been more sensitive to environmental change. Growth rates also decreased markedly from shallow to deeper water, as they do in present-day coral reefs. This decrease in growth rate is in response to the decreased intensity and quality of light which adversely affects the calcification process in corals.

Due to the more equable Jurassic climate, no systematic regional changes in the nature of the growth banding or the growth rate were seen. Data from outside this broad mid-latitude climatic belt could provide suitable material to assess the effect of regional changes in temperature and seasonality on the production of these growth bands. Such areas would include reefs developed farther south, for example in Portugal and North Africa, and to the north, in the Sub-Boreal Province, such as the corals from the Helmsdale region of northern Scotland. The low growth rates and L/H ratios recorded from the corals in Yorkshire are likely to be a response to the low solar radiation received at high palaeolatitudes, and are consistent with the Ziegler *et al.* (1984) model for the distribution of Bahamian-type carbonates.

Marked differences between the two species studied can be inferred in their ecophysiological behaviour, as reflected by variations in growth rate. Although *Isastraea explanata* had a greater growth rate, it shows little variation between different reef environments. *Thamasteria concinna*, on the other hand, had a lesser growth rate, though it shows a considerable variation between different reef types. It is suggested that this may be related to its strongly plastic ecomorphic behaviour.

This study has shown that it is possible to apply the methodology developed for present-day sclerochronology to Mesozoic Scleractinia. Moreover, the current concepts and ideas about the construction of present day corals seem also to apply to Mesozoic corals, which show similar growth behavioural patterns to modern forms. Thus Mesozoic sclerochronology is potentially an important tool for interpreting past environments and climates.

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